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Abstract: The Middle Jurassic is a largely mysterious interval in dinosaur evolution, as few fossils of this age are known worldwide. In recent years, the Isle of Skye has yielded a substantial record of trackways, and a more limited inventory of body fossils, that indicate a diverse fauna of Middle Jurassic dinosaurs living in and around lagoons and deltas. Comparatively little is known about the predators in these faunas (particularly theropod dinosaurs), as their fossils are among the rarest discoveries. We here report two new isolated theropod teeth, from the Valtos Sandstone and Lealt Shale Formations of Skye, which we visualized and measured using high-resolution x-ray computed microtomographic scanning (μCT) and identified via statistical and phylogenetic analyses of a large comparative dental dataset. We argue that these teeth most likely represent at least two theropod species—one small-bodied and the other large-bodied—which likely belonged to one or several clades of basal avetheropods (ceratosaurs, megalosauroids, or allosauroids). These groups, which were diversifying during the Middle Jurassic and would become dominant in Late Jurassic, filled various niches in the food chain of Skye, probably both on land and in the lagoons.

Introduction

Despite the flurry of new dinosaur discoveries across the globe over the last few decades, the Middle Jurassic remains a largely mysterious time for not only dinosaurs, but also terrestrial ecosystems in general. This is because very few Middle Jurassic localities preserve vertebrate fossils (e.g., Weishampel *et al*. 2004). One of these rare places is the Isle of Skye in Scotland, where deltaic and lagoonal sedimentary rocks of the Great Estuarine Group (Bathonian, ca. 168-166 million years old; Harris & Hudson 1980; Hudson 1993) are exposed. These yield trackways and bones of many types of dinosaurs (Andrews & Hudson 1984; Clark & Barco-Rodriguez 1998; Clark *et al.* 1995, 2004, 2005; Clark 2001; Liston 2004; Marshall 2005; Barrett 2006; Wills *et al*. 2014; Brusatte & Clark 2015; Brusatte *et al.*, 2015; Clark and Gavin, 2016; dePolo *et al*. 2018). They are associated with fossils of other tetrapods including mammals, and close relatives, crocodylomorphs, and turtles (Waldman and Savage 1972; Evans 2006; Anquetin *et al.* 2009; Wills *et al.* 2014; Young *et al.* 2016; Panciroli *et al.* 2017a, b, 2018; Yi *et al.* 2017).

Among the rarest dinosaur fossils from Skye are those of theropods, members of the mostly carnivorous group that includes iconic species like *Tyrannosaurus rex* and *Velociraptor*. Most Skye theropod fossils are footprints, made by small-to-mid-sized animals that probably stood about 1.0-2.5 metres tall at the hip. These have been described from several localities in the Lealt Shale, Valtos Sandstone, Duntulm, and Kilmaluag formations (Clark & Barco-Rodriguez 1998; Clark *et al*. 2004, 2005; Marshall 2005; dePolo *et al*. 2018), but provide limited information on the identity of the trackmakers. Bones of these animals are much less common, and thus far the only described theropod body fossils are a single tooth and a caudal vertebra, found separately but described together by Brusatte & Clark (2015), and part of a fragmentary theropod tooth described by Wills *et al*. (2014). A handful of teeth that have been

alluded to in the literature or in specimen lists are not yet described (e.g., Evans & Waldman 1996).

We here augment the patchy theropod record of Skye by describing two new isolated teeth, one of a small individual from the Valtos Sandstone and another of a larger theropod from the Lealt Shale, discovered in recent years during fieldwork conducted by the PalAlba group of collaborative Scottish institutions (Fig. 1). We use x-ray computed microtomographic (μCT) scanning to visualize and measure the teeth in detail. Comprehensive new datasets of theropod tooth measurements and cladistic characters of the dentition allow us to identify to which theropod groups they most likely belonged. We also use these new analyses to revisit the interpretation and classification of the most complete and best-preserved theropod tooth previously described from Skye, the specimen described by Brusatte & Clark (2015). Our results show that at least one, but probably several, species of theropod were present in Jurassic Skye, belonging to one or several clades of basal avetheropods (i.e., ceratosaurs, megalosauroids, or allosauroids).

Anatomical Abbreviations

AL, apical length; **CA**, crown angle; **CBL**, crown base; **CBR**, crown base ratio; **CBW**, crown base width; **CH**, crown height; **CHR**, crown height ratio; **CTU**, crown transverse undulation density; **DA**, distoapical denticle density; **DAVG**, average distal denticle density; **DB**, distobasal denticle density; **DC**, distocentral denticle density; **DDT**, dentine thickness distally; **DLAT**, dentine thickness labially; **DLIT**, dentine thickness lingually; **DMT**, dentine thickness mesially; **DSDI**, denticle size density index; **FABL**, fore-aft basal length; **LAF**, number of flutes on the labial surface of a crown; **LIF**, number of flutes on the lingual surface of a crown; **MA**, mesioapical denticle density; **MAVG**, average mesial denticle density; **MB**, mesio-basal denticle density; **MC**, mesiocentral denticle density; **MCE**, mesial carina extent; **MCL**, mid-

crown length; **MCR**, mid-crown ratio; **MCW**, mid-crown width; **MDE**, mesiobasal denticles extent.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York City, USA; **BP**, Evolutionary Studies Institute (formerly "Bernard Price Institute for Palaeontological Research"), University of the Witwatersrand, Johannesburg, South Africa; **CAGS**, Chinese Academy of Geological Sciences, Beijing, China; **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, USA; **FMNH**, Field Museum of Natural History, Chicago, USA; **GLAHM**, The Hunterian, University of Glasgow, Glasgow, Scotland, UK; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **JME**, Jura Museum Eichstätt, Eichstätt, Germany; **MACN**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MPC-D**, Institute of Paleontology and Geology, Mongolian Academy of Sciences (formerly IGM), Ulaanbaatar, Mongolia; **MUCPv**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh, USA; **NHMUK** PV, Natural History Museum, London, UK; **NMS**, National Museums of Scotland, Edinburgh, U.K.; **PVL**, Fundación 'Miguel Lillo,' San Miguel de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UMNH**, Natural History Museum of Utah, University of Utah, Salt Lake City, USA; **USNM**, United States National Museum Vertebrate Paleontology, National Museum of Natural History, Washington, District of Columbia, USA; **YPM**, Yale Peabody Museum of Natural History, Yale, Connecticut, USA.

Materials and Methods

Computed microtomography scanning

The two teeth are catalogued at National Museums Scotland: the large Lealt specimen as NMS G.2018.17.1 and the small Valtos specimen as NMS G.2018.17.2. We subjected both teeth to X-ray computed microtomography (μCT) scanning at the School of GeoSciences, University of Edinburgh. Data for NMS G.2018.17.1 and NMS G.2018.17.2 were acquired at peak energies of 130 keV and 70 keV, respectively, each filtered with a 0.3 mm thick Al energy filter. Reconstruction of the scans (both comprising 2000 projection images) used Octopus v8.9 software (Vlassenbroek *et al*. 2010) to yield tomographic slices with a geometric resolution of 68 μm for NMS G.2018.17.1 and 20μm for NMS G.2018.17.2. We used the μCT slices to construct 3D digital models of both teeth using Mimics 19.0 (Materialize N.V. 2014) and digitally measured them for standard variables (see below). We confirmed these measurements, and assessed other details of the morphology, by examining the teeth under a binocular microscope.

Comparative methodology and terminology

For both teeth, we took up to six measurement variables (i.e., CBL, CH, MA, MC, DC, DA; Table 1) on the crowns, either physically on the specimens with calipers or, for those measurements of portions of the teeth still obscured by matrix, digitally using the models in Mimics 19.0 and calipers. We estimated values of CBL and AL in NMS G.2018.17.1 based on the curvature of the mesial profile. We added these measurements to a comparative dataset, which includes information on the dentition of 155 non-avian theropod species-level taxa,

among which 118 were examined first hand in 35 collections in Argentina, France, Belgium, Germany, Italy, Portugal, Qatar, Switzerland, the United Kingdom, South Africa, China, Canada and the USA by C. Hendrickx (Supplementary Appendix 1). In constructing this dataset, C. Hendrickx used an AM411T-Dino-Lite Pro digital microscope to observe denticles, crown ornamentations, enamel texture and small teeth. We followed the dental nomenclature and method proposed by Hendrickx *et al*. (2015a) to describe each tooth comprehensively. Morphometric and anatomical terms and abbreviations follow those defined by Smith *et al*. (2005) and Hendrickx *et al*. (2015a). The terminology of anatomical orientations follows the recommendations of Smith & Dodson (2003) and Hendrickx *et al*. (2015a). We also use the specimens observed to construct the dataset to make qualitative comparisons with the Skye teeth in the descriptive section.

Cladistic analysis

In order to explore their phylogenetic affinities, we scored NMS G.2018.17.1 and NMS G.2018.17.2 separately into an updated version of the dentition-based cladistic data matrix of Hendrickx & Mateus (2014a). The data matrix includes 145 discrete characters scored across 95 genus-level operational taxonomic units (OTUs) phylogenetically bracketed between the basal sauropodomorph *Eoraptor lunensis* (Sereno *et al*. 1993, 2013) and the basal avialan *Archaeopteryx lithographica* (Meyer 1861; Howgate 1984; Rauhut 2014; Rauhut *et al*. 2018; Supplementary Appendix 2). We also included a third theropod tooth from the Jurassic of the Isle of Skye, GLAHM 125390a, previously described by Brusatte & Clark (2015), in the data matrix. Because it is not clear if the three Skye teeth are mesial or lateral teeth, we scored each one as a mesial tooth for mesial characters, then separately as a lateral crown for lateral characters, and then conducted multiple phylogenetic analyses. We performed these cladistic

158 analyses using TNT 1.1 (Goloboff *et al*. 2008) and a positive constraint (force + command)
159 based on a backbone topology, setting the three Skye teeth as floating OTUs (Supplementary
160 Appendix 2). The backbone tree topology was based on the results obtained by the following
161 analyses: Müller *et al*. (2018) in their fifth analysis (i.e., analysis conducted on the data matrix
162 of Baron *et al*. [2017] using Langer *et al*.'s [2017] modifications) for non-averostran theropods;
163 Rauhut & Carrano (2016) and Wang *et al*. (2017) for Ceratosauria; Carrano *et al*. (2012) and
164 Rauhut *et al*. (2016) for non-coelurosaurian tetanurans; Brusatte & Carr (2016) for
165 Tyrannosauroidea; and Cau *et al*. (2017), in part, based on the dataset of Brusatte *et al*. (2014),
166 for non-tyrannosauroid coelurosaurs. The analyses were conducted using a combination of
167 tree-search algorithms: Wagner trees, TBR branch swapping, sectorial searches, Ratchet
168 (perturbation phase stopped after 20 substitutions), and Tree Fusing (5 rounds), until 100 hits
169 of the same minimum tree length were achieved. The best trees obtained were subjected to a
170 final round of TBR branch swapping (i.e., xmult = hits 100 rss fuse 5 ratchet 20 followed by
171 the bb commands).
172
173 ***Discriminant analysis***
174
175 In order to use measurement data to predict their optimal classifications into major theropod
176 groups, we included NMS G.2018.17.1 and GLAHM 125390a in a quantitative dataset (based
177 on Hendrickx et al. 2015b) that we subjected to discriminant function analysis (DFA). NMS
178 G.2018.17.2, consisting of the tip of a crown, was not included in the DFA given that only a
179 single variable (DA) was measurable.
180 Hendrickx *et al*.'s (2015b) dataset initially included 11 measurements (i.e., CBL, CBW,
181 CH, AL, CBR, CHR, MCL, MCW, MCR, MC, and DC—see 'Anatomical Abbreviations'
182 above for definitions) for 995 teeth belonging to 62 non-avian theropod taxa. The dataset

combines morphometric data collected by Smith & Lamanna (2006) and Larson & Currie (2013) that incorporate measurements by Smith (2005), Sankey *et al*. (2002), and Longrich (2008) (see Hendrickx *et al*. (2015b) and references therein). We supplemented Hendrickx *et al*.'s (2015b) dataset with measurements provided by Longrich *et al*. (2017) for *Chenanisaurus*, Malafaia *et al*. (2017a,b) for *Torvosaurus*, Richter *et al*. (2013) for an indeterminate Spinosaurinae, Currie & Azuma (2006) for *Fukuiraptor*, Hocknull *et al*. (2009) and White *et al*. (2015) for *Australovenator*, Gerke & Wings (2016) for *Proceratosaurus*, Zanno *et al*. (2016) for *Eshanosaurus*, Evans *et al*. (2013) for *Acheroraptor*, and Gianechini *et al*. (2011) for *Buitreraptor*. In all, we added 257 teeth belonging to 39 taxa to Hendrickx *et al*.'s (2015b) dataset, based on first hand measurements of the crowns following the methodology of Hendrickx *et al*. (2015a).

The final dataset (here entitled 'whole dataset') includes 15 measurements (i.e., CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MSL, LAF, LIF, CA, MDL, DCL) for 1,291 teeth belonging to 75 taxa (i.e., 71 species and four indeterminate family-based taxa), representing the most taxon-rich theropod tooth dataset currently available (Supplementary Appendix 1). New measurements in this dataset, relative to Hendrickx *et al*. (2015b), include the extension of the denticulate mesial carina (= mesial serrated carina length: MSL), the crown angle (CA), and the number of flutes on the labial (LAF) and lingual (LIF) surfaces of the crown. We used MDL and DCL instead of the MC and DC metrics of Smith et *al*. (2015) and Hendrickx *et al*. (2015b), to ensure that the dataset mostly includes metric-based variables. Likewise, the variables CA, MCL and DCL were not size-corrected, because the crown angle does not change with tooth dimension and because denticle size varies independently from crown height and thickness. All variables were log-transformed to approach a normal distribution (Samman *et al*. 2005; Smith 2005; Larson & Currie 2013) and a log(x+1) correction was applied to LAF and LIF to account for the absence of flutes on the crown. This

formula was also used by Gerke & Wings (2016) for MC and DC to account for unserrated carinae. Nevertheless, a crown without denticles should not be morphometrically closer to those with a low number of denticles (i.e., 5 or 6 denticles per five mm, as present in *Tyrannosaurus* or *Torvosaurus*). This is, in fact, the opposite of what we would expect, because theropods with unserrated teeth appear to evolve from taxa with many minute denticles (n.b., Parvicursorinae and Caudipteridae with unserrated teeth evolved from *Haplocheirus* and *Incisivosaurus*-like theropods, respectively, with a large number of minute denticles on their carinae; C. H. pers. obs.). As a result, an arbitrary value of 100 denticles per five mm was used for unserrated carinae based on the fact that taxa that possess both denticulated and unserrated teeth in the same jaw (e.g., *Compsognathus*, *Aorun*, *Haplocheirus*, *Incisivosaurus*; MNHN CNJ79, IVPP V15709; IVPP V14988; IVPP V13326) typically bear more than ten denticles per mm on the carinae.

We performed six discriminant function analyses (DFAs) on partitions of our dataset. In all cases, only non-ratio variables and taxa that could be assessed for at least four measurement variables were used in our DFAs. A first DFA on the whole dataset used twelve variables (i.e., CBL, CBW, CH, AL, MCL, MCW, MSL, LAF, LIF, CA, MDL, and DDL). Because different authors have measured theropod crowns in slightly different ways (CBL and CH specially; see Gerke & Wings, 2016), we performed a second DFA on a dataset (here entitled 'personal dataset') restricted to our own measurements. Our personal dataset includes 550 teeth belonging to 71 taxa gathered into 20 groups (i.e., basal-most Theropoda, non-averostran Neotheropoda, non-abelisauroid Ceratosauria, Noasauridae, Abelisauridae, non-megalosaurian Megalosauroidea, Megalosauridae, Spinosauridae, Metriacanthosauridae, Allosauridae, Neovenatoridae, Carcharodontosauridae, basal Coelurosauria, non-tyrannosaurid Tyrannosauroidea, Tyrannosauridae, Compsognathidae, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae). Given the large size of NMS G.2018.17.1,

a third and fourth DFA were conducted on the whole dataset and our own dataset, but restricted to taxa with large-sized crowns (i.e., CH > 20 mm). These two datasets include 701 and 375 teeth belonging to 51 and 44 large-sized theropod taxa, respectively. We finally performed fifth and sixth DFAs based on the datasets of Smith *et al*. (2005), using the variables CBL, CBW, CH, AL, CA, CA2, MC, DC, MAVG, DAVG and DAVG2, and Gerke & Wings (2016), using CBW, CH, AL, MC, DC and CBL or CHR. DFAs were conducted in PAST v3.19 (Hammer et al. 2001) with the Discriminant analysis (LDA) function. NMS G.2018.17.1 and GLAHM 125390a were considered as the unknown taxon in each analysis and classified at genus or group-level.

Results

Cladistic analysis

The cladistic analysis of the dentition-based data matrix (Supplementary Appendix 2) with NMS G.2018.17.1 as the floating OTU yielded twelve most parsimonious trees (MPTs) when scored as a mesial tooth (Consistency Index (CI) = 0.212; Retention Index (RI) = 0.461; Length = 1211) and five most parsimonious trees when scored as a lateral tooth (CI = 0.212; RI = 0.461; Length = 1211). Scored as a mesial crown, NMS G.2018.17.1 occupied various positions among non-abelisauroid Ceratosauria and Megalosauridae, or as the basal-most Tetanurae, Megalosauroidea or Avetheropoda. Scored as a lateral tooth, it was placed among Ceratosauria, as the basal-most taxon of the clades *Berberosaurus* + Ceratosauridae or Abelisauroidea, among Megalosauroidea, closely related to *Monolophosaurus* or *Sciurumimus*, or as the basal-most Allosauroidea (Figure 2).

The analysis with NMS G.2018.17.2 as the floating OTU yielded three MPTs when scored as a mesial tooth (CI = 0.212; RI = 0.462; Length = 1211) and a single MPT (CI = 0.212; RI = 0.461; Length = 1212) when scored as a lateral tooth. As a lateral crown, NMS G.2018.17.2 was found as the sister taxon of *Velociraptor* among Dromaeosauridae. On the other hand, when scored as a mesial crown, NMS G.2018.17.2 was recovered either as a taxon more basal than *Daemonosaurus* among non-theropod Saurischia or as the sister taxon of *Limusaurus* among Noasauridae.

The analysis with GLAHM 125390a as the floating taxon yielded a single MPT when coded as a mesial (CI = 0.212; RI = 0.462; Length = 1212) and a lateral tooth (CI = 0.212; RI = 0.461; Length = 1213). In the latter analysis, GLAHM 125390a was placed as the sister taxon of *Tsaagan* among Dromaeosauridae (Figure 2), whereas the specimen was recovered as the sister taxon of *Megaraptor* among Megaraptora as a mesial crown.

Discriminant analysis

Results of the various DFAs, summarized in Table 1 and detailed in Supplementary Appendix 4, show no consistent placement of either NMS G.2018.17.1 or GLAHM 125390a, at the group level or the taxon level. The two isolated teeth are recovered outside the morphospace occupied by other theropods in the DFA performed on the whole dataset (Appendix 4), whereas GLAHM 125390a was retrieved within the morphospace occupation of non-abelisaurid ceratosaurs and non-spinosaurid megalosauroids in the analysis performed using our personal dataset (Figure 3). Both teeth are assigned to distantly related clades or taxa such as *Dilophosaurus*, Ceratosauridae, non-abelisauroid Ceratosauria, *Torvosaurus*, *Suchomimus*, Metriacanthosauridae, Neovenatoridae, Carcharodontosauridae, and

Troodontidae (Appendix 4). However, we note that the most common assignments for both teeth are within the non-coelurosaurian groups of Ceratosauria and Allosauroidea (Table 1).

Systematic Palaeontology

Dinosauria Owen 1842

Saurischia Seeley 1887

Theropoda Marsh 1881

Neotheropoda Bakker 1986

Gen. and sp. indet.

(Fig. 2)

Material. NMS G.2018.17.2, an incomplete isolated tooth preserving part of the crown apex. The apical-most and basal parts of the crown, as well as the root and most of the lingual portion of the crown apex, are missing (Fig. 2K-P). The outline of the tip is visible as an impression in the matrix. The labial surface is exposed from the matrix, and both mesial and distal edges are visible. Details of the hidden surfaces are observable in the CT scans (Fig. 2N-R). The labial surface is well preserved in most places, but the base of the preserved portion of the crown is highly fractured.

Provenance. The tooth was discovered by T. Challands in an ex-situ block of the Middle Jurassic Valtos Sandstone Formation at Brothers' Point (Rubha nam Brathairean), NG 573513.20N 692.98W.

Description. NMS G.2018.17.2 is the apex of a medium-size crown, likely more than 15 millimetres in apicobasal height (Fig. 2). Its key measurements are listed in Supplementary Appendix 1. The crown is nearly triangular in shape, with a slight distal recurvature. The mesial edge is weakly convex and the distal edge is ever so slightly concave. The labial side of the crown apex is asymmetrically convex in apical view; i.e., the surface is gently convex on the distal two-thirds of the crown and strongly convex on the mesial third (Fig. 1Q). The distal carina is serrated along its entire length, whereas the mesial carina is smooth and lacks serrations (Fig. 1Q, P). The distal carina is strongly labially displaced and appears to extend closer to the labial surface basally (Fig. 1Q, O). We counted 20 denticles per five millimeters on the preserved portion of the distal carina. The distal denticles are labiolingually elongated, perpendicular to the distal margin, and separated by broad interdenticular spaces. The external margin of each denticle is symmetrically to asymmetrically convex, but not apically hooked. No interdenticular sulci extend from between the denticles. The external enamel surface is smooth and lacks any substantial ornamentation, texturing, ridges, grooves, flutes, or undulations.

Identification. NMS G.2018.17.2 is assigned to a non-sauropodomorph saurischian based on the finger-like shape of its distal denticles, the strongly labially deflected distal carina and the presence of an unserrated mesial carina. To our knowledge, the teeth of ornithischians, sauropodomorphs, marine reptiles, pterosaurs and crocodylomorphs do not share such morphology, a combination of unserrated mesial carina, mesiodistally elongated finger-like distal denticles and broad interdenticular sulci has never been observed in any of these clades, to our knowledge.

Based on the large size of the basal distal denticles NMS G.2018.17.2 is likely only a part of the crown apex of a tooth. In non-sauropodomorph saurischians, the mesial and distal

denticles typically decrease in mesiodistal height and apicobasal width towards the base of the crown (Farlow et al. 1991). Only some teeth of some theropods (e.g., *Noasaurus*, *Juravenator*, *Microraptor* and *Sinusonasus*; PVL 4061; JME Sch 200; CAGS 20-7-004; IVPP V11527) have the same denticle density at the basal-most and central parts of the distal carinae. However, their basal-most denticles are always apicobasally subrectangular and not mesiodistally elongated as in NMS G.2018.17.2. Given that the preserved portion of the crown of NMS G.2018.17.2 is ~7 mm in height, and based on the size of the denticles, the crown height was likely higher than 15 millimetres. Consequently, accurate measurements are not possible for crown height (CH), crown-base length and width (CBL and CBW), and crown-compression and elongation (CBR and CHR). This makes it more difficult for the quantitative analyses to robustly identify which clade this tooth belonged to.

Nevertheless, NMS G.2018.17.2 displays four important features that give insight into its affinities: labiolingually elongated distal denticles perpendicular to the distal margin, a broad interdenticular space separating the distal denticles, a strongly labially deflected distal carina and an unserrated mesial carina.

The presence of labiolingually elongated, finger-like distal denticles with symmetrically convex external margins exclude an ornithomimosaur, alvarezsaurid, therizinosaurid, oviraptorosaur, troodontid, or avialan affinity for NMS G.2018.17.2. Many members of these clades lack serrated teeth, but when such teeth are present, they have either many more than 20 denticles per 5 mm on the carinae (e.g., *Falcarius*, *Incisivosaurus*, and *Sinusonasus*; UMNH VP 14545; IVPP V13326; IVPP V11527) or apically inclined/hooked denticles (e.g., therizinosauroids and some derived troodontids; Currie et al. 1990; Currie & Dong 2001; Zanno et al. 2016).

Broad interdenticular spaces like those in NMS G.2018.17.2 are also seen in non-averostran theropods (e.g., *Herrerasaurus, Dracoraptor*; PVSJ 407; BP/1/5243), non-

abelisauroid ceratosaurs (e.g., *Ceratosaurus*, *Genyodectes*; UMNH VP 5278; MLP 26-39), non-megalosaurian megalosauroid (e.g., *Marshosaurus*, *Monolophosaurus*; DMNH 3718; IVPP 84019), allosauroids (e.g., *Sinraptor*, *Allosaurus*, *Acrocanthosaurus*; IVPP V10600; USNM 8335; UMNH VP 6499; NCSM 14345), tyrannosauroids (e.g., *Guanlong*, *Gorgosaurus*; IVPP V14531; RTMP 1991.36.500) and some dromaeosaurids such as *Bambiraptor* (AMNH 30556) and *Deinonychus* (YPM 5232). However, this space is narrow in Abelisauroidea and Spinosauridae, and we consider it unlikely that NMS G.2018.17.2 belongs to one of these clades.

Teeth with a strongly labially displaced distal carina are present in the mesial and/or lateral dentition of some non-averostran saurischians (e.g., *Ischisaurus*; MACN 18.060), non-abelisaurid ceratosaurs (e.g., *Genyodectes*, *Masiakasaurus*; MLP 26-39, FMNH PR 2476), piatnitzkysaurids (e.g., *Piatnitzkysaurus*; MACN 895), *Monolophosaurus* (IVPP 84019), allosauroids (e.g., *Acrocanthosaurus*, *Giganotosaurus*; NCSM 14345, MUCPv-CH-1), tyrannosauroids (e.g., *Proceratosaurus*, *Alioramus*; NHMUK PV R.4860, MPC-D 100-1844), and dromaeosaurids (e.g., *Sinornithosaurus*, *Linheraptor*; IVPP V12811, V16923). A broad interdenticular space and a strongly labially displaced distal carina appear to be absent in Abelisauridae, Megalosauridae and Spinosauridae, so NMS G.2018.17.2 most likely does not belong to these clades.

Finally, the unserrated mesial carina, combined with a denticulated distal carina, is a condition restricted to the mesial and/or lateral dentition of non-neotheropod theropods (e.g., *Herrerasaurus*, *Ischisaurus*; PVSJ 407, PVSJ 605), noasaurids (e.g., *Masiakasaurus*; FMNH PR 2476), the juvenile megalosaurid *Sciurumimus* (Rauhut et al. 2012), megaraptorans (e.g., *Megaraptor*; Porfiri et al. 2014), some basal tyrannosauroids (e.g., *Dilong*; IVPP V14242) compsognathids (e.g., Currie & Chen 2001; Peyer 2006; Dal Sasso & Maganuco 2011), basal maniraptoriforms (e.g., *Aorun*, *Ornitholestes*, *Haplocheirus*; AMNH 619; Choiniere et al.

2014*b*, *b*), and many dromaeosaurids (e.g., Currie et al. 1990; Norell et al. 2006; Godefroit et al. 2008) and troodontids (e.g., Currie 1987; Currie and Dong 2001; Norell et al. 2009). These are therefore all candidate clades for NMS G.2018.17.2.

The cladistic analysis indicates that NMS G.2018.17.2 may belong to a non-neotheropod saurischian, a noasaurid closely related to *Limusaurus* or a dromaeosaurid. We argue that the first clade is unlikely based on the Middle Jurassic age of NMS G.2018.17.2. Among non-sauropodomorph saurischians, neotheropods such as non-spinosaurid megalosauroids are the only clade present in the Middle Jurassic with a dental morphology similar to that of NMS G.2018.17.2 (Hendrickx et al. 2015*a*, *b*; Rauhut et al. 2016). To our knowledge, no Jurassic sauropodomorphs have teeth with finger-like denticles and a strongly labially deflected mesial carina. Furthermore, based on current theropod phylogenies (e.g., Müller *et al*. 2018; Baron *et al*. 2017; Wang *et al*. 2017), non-neotheropod theropods are restricted to the Late Triassic and Early Jurassic.

Although Dromaeosauridae might be present in the Middle Jurassic, based on ghost lineages (Hendrickx *et al*. 2015), a dromaeosaurid affinity for NMS G.2018.17.2 may be unlikely, given that denticles were absent from the teeth of most basal members of the group (Gianechini *et al*. 2011; Cau *et al*. 2017). Unserrated teeth are, in fact, likely to be the plesiomorphic condition among the derived clade of bird-like theropods that includes dromaeosaurids and close relatives (Pennaraptora or Paraves), pending the position of scansoriopterygids at the base of Oviraptorosauria or Avialae (Brusatte *et al*. 2014; Cau *et al*. 2017). We here hypothesize that most, if not all, Middle Jurassic dromaeosaurids, unlike non-maniraptoriform neocoelurosaurs and noasaurids, had unserrated teeth. There have been serrated teeth from Middle Jurassic deposits assigned to dromaeosaurids based on broad resemblance (e.g., Evans & Milner 1994; Metcalf & Walker 1994; Averianov *et al*. 2005), but

404 these could plausibly belong to non-maniraptoriform theropods with similar dental
405 morphologies, such as basal tyrannosauroids (Rauhut *et al*. 2010).

406 The combination of dental features in NMS G.2018.17.2, the distribution of these
407 features among non-sauropodomorph saurischians, and the results of the cladistic analysis,
408 indicate that NMS G.2018.17.2 may tentatively be attributed to either: 1) a neotheropod
409 theropod other than a member of Abelisauridae, Megalosauria and Maniraptoriformes, or 2)
410 possibly a ceratosaur closely related to Noasauridae.

411

412 Averostra Paul 2002

413 Gen. and sp. indet.

414 (Fig. 2)

415

416 *Material*. NMS G.2018.17.1, an isolated tooth preserving most of the crown but missing the
417 root. The lingual surface of the crown is exposed from the matrix, and both mesial and distal
418 edges are visible. Details of the labial surfaces are observable in the CT scans (Fig. 2F). The
419 lingual surface is well preserved towards the apex, but the base of the crown is highly fractured
420 and much of the enamel layer has been worn away so that the cervix (i.e., the limit between
421 crown and root) cannot be seen (Fig. 2A-B, E). There are no denticles in either the basal two-
422 thirds of the mesial carina or basal one third of the distal carina (Fig. 2A). The reconstructed
423 3D CT model of the tooth shows that the labial surface is more complete than the lingual one.
424 However, the mesial portion and most of the mesiobasal part of the labial surface of the crown
425 are not preserved (Fig. 2F).

426

427 *Provenance*. The tooth was discovered by D. Foffa in an in-situ portion of the Middle Jurassic
428 Lealt Shale Formation exposed as a tidal platform, at Brothers' Point (Rubha nam Brathairean).

Much of the labial/lingual side of the tooth was visible on the surface when collected, but the tip of the apex was covered by matrix and later exposed through manual preparation by T. Challands.

Description. NMS G.2018.17.1 is a large (~6 cm in height), ziphodont, and distally recurved crown. Its key measurements are listed in Supplementary Appendix 1. The mesial edge is convex and the distal edge concave in lateral and medial views, whereas the preserved labial and lingual surfaces are symmetrically convex in apical and basal views (Fig. 1I, J). Both mesial and distal carinae are denticulated and extend to the apex, which is crossed by denticles (Fig. 1B, C). The mesial carina is denticulated along its preserved portion, but it is not clear if denticles reached close to the cervix, or terminated at mid-crown. The mesial carina appears to curve slightly mesiolingually towards the base of the crown, as seen in mesial (Fig. 1I) and apical (Fig. 1G) views. The distal carina is apicobasally straight all along the crown, in distal view (Fig. 1H). Although the distal carina appears to be deflected lingually due to the large missing portion of the lingual surface of the crown (Fig. 1I), the carina is centrally positioned on the crown in apical view (Fig. 1I). The distal denticles are better preserved than those on the mesial carina, where denticle apices are largely eroded. We counted 11 denticles per five millimeters on the mesiocentral, distocentral and distoapical portions of the carinae, and 12 denticles per five millimeters in the apical-most part of the mesial carina. There is, therefore, no size discrepancy between mesial and distal denticles (i.e., Denticle Size Density Index (DSDI) close to 1; Rauhut & Werner 1995). The distal denticles are weakly mesiodistally subrectangular in the central portion of the carina and subquadrangular more apically. The external margins of the preserved distal denticles are symmetrically convex. There are broad interdenticular spaces between the distal denticles and no interdenticular sulci. The tooth appears to be fairly thin in cross section, although accurate measurements are not possible due

454 to the heavy damage incurred on the exposed surface. There is no strong ornamentation on the
455 exposed enamel surfaces, nor those visible in the CT scans.
456
457 *Identification*. NMS G.2018.17.1 is identified as a theropod based on a combination of features
458 that, to our knowledge, are restricted to theropods among Middle Jurassic tetrapods: large size
459 (~6 cm in height), distally recurved crown, both carinae bearing denticles (with fewer than 15
460 denticles per 5 mm on both carinae), and weakly lingually twisted mesial carina.
461 The discriminant function analyses place NMS G.2018.17.1 outside of the
462 morphospace envelope for all other theropod teeth in our dataset, an unexpected finding.
463 However, this is likely due to the limited measurement data available for the tooth, particularly
464 the absence of data for crown compression, combined with estimated values for CBW and AL.
465 Therefore, results of the discriminant analyses should be considered as highly tentative. These
466 place NMS G.2018.17.1 in a variety of possible theropod clades, including as a dilophosaurid
467 (*Dilophosaurus*), a non-abelisauroid ceratosaur, a ceratosaurid, an abelisaurid (*Rugops* or
468 *Arcovenator*), a megalosaurid (*Torvosaurus*), a neovenatorid, a carcharodontosaurid, and even
469 a troodontid.
470 NMS G.2018.17.1, however, does possess several important qualitative features that
471 help constrain its most likely identification (Hendrickx *et al*. 2015b; Hendrickx & Mateus
472 2014). Given that NMS G.2018.17.1 is a ziphodont tooth (i.e., it is a distally recurved crown
473 with denticulated mesial and distal carinae) of particularly large size (i.e., ~6 cm), based on our
474 current knowledge it cannot be from a member of Noasauridae, Compsognathidae,
475 Ornithomimosauria, Therizinosauria, Alvarezsauroidea, Oviraptorosauria, Dromaeosauridae,
476 Troodontidae, or Avialae. To our knowledge, members of these clades all bear finely
477 denticulated or unserrated non-ziphodont teeth (i.e., conidont, folidont teeth) or small
478 ziphodont teeth less than five centimetres long apicobasally.

Among ziphodont theropods, NMS G.2018.17.1 displays several key features with taxonomic utility, including broad interdenticular spaces between the distal denticles, a centrally positioned distal carina, a weakly lingually twisted mesial carina, fewer than 15 mesial and distal denticles, and a DSDI close to one. Broad interdenticular spaces between distal denticles are present in non-averostran theropods, non-abelisauroid ceratosaurs, non-megalosaurian megalosauroid (i.e., Piatnitzkysauridae, *Monolophosaurus* and *Sciurumimus*), most allosauroids and many tyrannosauroids (Hendrickx and Mateus' (2014) datamatrix). Because the crown is relatively compressed labiolingually (i.e., CBR < 0.65) and because the mesial carina neither twists conspicuously mesiolingually nor is strongly displaced lingually, NMS G.2018.17.1 cannot be from the mesial dentition of Ceratosauria, non-carcharodontosaurid Allosauroidea (i.e., Metricanthosauridae and Allosauridae) or Tyrannosauroidea. Teeth with fewer than 15 denticles per 5 mm are present in ceratosaurs, megalosauroids, allosauroids, and large-sized tyrannosauroids such as tyrannosaurids. Non-averostran theropods other than herrerasaurids seem not to have teeth with fewer than 15 denticles per 5 mm on the distal carina (Hendrickx and Mateus' (2014) datamatrix). Finally, with a DSDI close to one, NMS G.2018.17.1 probably does not belong to a piatnitzkysaurid or a basal tyrannosauroid, as most members of these clades have crowns whose mesial denticles are significantly smaller than those on the distal carina (Rauhut et al. 2010).

The combination of dental features displayed by NMS G.2018.17.1, suggests that this large crown may belong to the mesial/lateral dentition of a non-noasaurid and non-abelisaurid ceratosaur; to the mesial dentition of a megalosaurid or a basal tetanuran/megalosauroid/avetheropod; or to the lateral dentition of a non-megalosaurian megalosauroid closely related to *Monolophosaurus* or a basal allosauroid. The results of the cladistic analysis, combined with the Middle Jurassic age and northern European provenance of the tooth, suggest that the specimen almost certainly belongs to an averostran theropod, and

504 we favour a non-abelisauroid ceratosaur, a basal megalosauroid closely related to
505 *Monolophosaurus*, a megalosaurid or an allosauroid as most likely. Nonetheless, it is possible
506 that the tooth belongs to another theropod clade with similar tooth morphologies, such as
507 Tyrannosauroidea. Middle Jurassic tyrannosauroids have, been identified recently, albeit of
508 small size (Averianov *et al*. 2010; Rauhut *et al*. 2010), so NMS G.2018.17.1 could conceivably
509 belong to this group.
510
511 **Revision of GLAHM 125390a**
512
513 This specimen, GLAHM 125390a, the most complete and well-preserved theropod tooth
514 described from the Isle of Skye, was first reported and thoroughly described by Brusatte &
515 Clark (2015). The shed tooth comes from the Valtos Sandstone, the same formation that yielded
516 NMS G.2018.17.2. However, GLAHM 125390a was found at Valtos, approximately one mile
517 north of Brother's Point, where NMS G.2018.17.2 was discovered. Based on a series of
518 quantitative analyses Brusatte & Clark (2015) referred GLAHM 125390a to Theropoda indet.,
519 suggesting that it most likely belongs to a dromaeosaurid, a megalosaurid, a basal
520 tyrannosauroid or a small-bodied basal coelurosaur.
521 We included GLAHM 125390a within our larger datasets and conducted a series of
522 new DFAs and cladistic analyses. The DFAs on our whole dataset, our dataset of personal
523 measurements, and the datasets of Smith & Lamanna (2006) and Gerke & Wings (2016)
524 classify GLAHM 125390a as either a troodontid, ceratosaurid, neovenatorid or a
525 carcharodontosaurid at the group level. At the taxon level, GLAHM 125390a was assigned to
526 the abelisaurids *Rugops* and *Majungasaurus*, as well as *Ceratosaurus*, *Suchomimus*,
527 *Neovenator* and *Megaraptor*. In the cladistic analysis, GLAHM 125390a is positioned as a

528 dromaeosaurid closely related to *Tsaagan* or as the sister taxon of *Megaraptor* within
529 Megaraptora (when coded as a mesial and lateral tooth, respectively).

530 Brusatte & Clark (2015) also used cladistic analysis and, coding GLAHM 125390a as
531 a lateral tooth, recovered a tree with a large polytomy that differs from the well-resolved tree
532 obtained in this study. This is because the specimen was scored slightly differently in our data
533 matrix, having subtle transverse undulations on the crown, a higher number of distal denticles
534 apically than at mid-crown, and distal denticles perpendicular to the distal margin. The apically
535 inclined distal denticles noted by Brusatte & Clark (2015) are an illusion due to interdenticular
536 sulci that curve basally. The presence of a constriction between the root and crown was coded
537 as unknown in our dataset. Although there is indeed no constriction at the cervix on the distal
538 profile of the crown, the mesiobasal portion is not preserved in GLAHM 125390a, so the
539 presence of a mesial constriction, as seen in most folidont theropods, cannot be ruled out.
540 Finally, interdenticular sulci appear to be particularly well-developed between mid-crown
541 denticles of the distal carina, so that both short and long denticular sulci were scored as present
542 in our data matrix.

543 Brusatte & Clark (2015) identified GLAHM 125390a as belonging to an indeterminate
544 theropod, but the clade can now be narrowed to Neotheropoda. Strongly developed and
545 elongated interdenticular sulci appear to be restricted to non-neocoelurosaur averostrans and
546 therizinosaurs. A therizinosaur affinity is excluded on the basis of the presence of mesiodistally
547 elongated distal denticles perpendicular to the distal margin of the crown, the absence of a
548 convex distal profile of the crown, and a distal constriction between crown and root. However,
549 strongly developed interdenticular sulci may be present in neotheropods, such as
550 dilophosaurids. Similar to the wide interdenticular space (see above), an irregular enamel
551 texture is seen in distantly related clades such as herrerasaurids, abelisauroids, allosaurids,
552 metriacanthosaurids, some tyrannosaurids and most non-dromaeosaurid neocoelurosaurs.

553 Because the status of the mesial denticles and a mesial constriction between root and crown
554 are unknown, and given the limited amount of dental information available and the age of the
555 specimen, GLAHM 125390a is, therefore, referred to an indeterminate neotheropod.

556 Unlike Brusatte and Clark (2015), we are not as confident that GLAHM 125390a
557 belongs to one of three groups (a megalosaurid, a non-tyrannosaurid tyrannosauroid, or a
558 dromaeosaurid). The features do not correspond perfectly to any of these three clades. For
559 instance, the crowns of megalosaurids and non-tyrannosaurid tyrannosauroids all display a
560 braided enamel texture, whereas dromaeosaurids do not seem to have elongated interdenticular
561 sulci between distal denticles to our knowledge. Given the combination of dental features
562 displayed by GLAHM 125390a, it is also possible that the specimen belongs to a ceratosaur
563 (i.e., Ceratosauridae, Abelisauridae, and Noasauridae), or a basal allosauroid (i.e.,
564 Metriacanthosauridae, Allosauridae). It is also possible that it belongs to the same taxon as
565 NMS G.2018.17.1 and/or NMS G.2018.17.2 (see below).

566

567 **Theropod Diversity on Skye**

568

569 How many species are represented by the three teeth described above? This question is difficult
570 to answer conclusively, but there are several lines of evidence. The three teeth all differ from
571 each other, most notably in crown height, distal denticle density, the presence of well-
572 developed interdenticular sulci between distal denticles, the denticulation of the mesial carina,
573 and the position of the distal carina on the distal surface of the crown (i.e., strongly displaced
574 in NMS G.2018.17.2, but centrally positioned in GLAHM 125390a and NMS G.2018.17.1).
575 Whether these differences are taxonomically informative is less clear, because many dental
576 features are ontogenetically dependant (e.g., the size of mesial and distal denticles; Carr and
577 Williamson 2004), and the development of interdenticular sulci and position of the carina on

578 the distal surface are variable along the tooth-row of individuals (e.g., Smith 2005; Benson
579 2009; Reichel 2012; Hendrickx et al. 2015). It could be, therefore, that the differences between
580 the three teeth reflect a combination of ontogenetic and/or individual variation among one or
581 two species, rather than signifying three distinct theropod species.

582 There are two main arguments against the three teeth belonging to the same species:
583 differences in carina denticulation and differences in size. NMS G.2018.17.2 lacks denticles
584 on the mesial carina, whereas NMS G.2018.17.1 and GLAHM 125390a both have a
585 denticulated mesial carina. However, some theropods such as *Coelophysis* (Buckley & Currie
586 2014) and *Ornitholestes* (AMNH 619) have some mesial teeth devoid of a mesial carina,
587 whereas mesial denticles are present in at least some lateral teeth. Thus, this difference alone
588 does not indicate species-level separation.

589 Even more striking, however, is the enormous size difference between the tiny tooth
590 NMS G.2018.17.2 and the other two Skye teeth. It is doubtful that these teeth could belong to
591 individuals of the same general body size, although it is possible that NMS G.2018.17.2 is from
592 an extremely young juvenile and NMS G.2018.17.1 and GLAHM 125390a from more mature
593 individuals. This seems implausible, however, as the adult would be a medium-to-large-bodied
594 theropod, and the vast majority of such species (with teeth longer than 6 cm in adults) exhibit
595 mesial denticles in both mesial and lateral teeth (C. H. pers. obs.). There is only one known
596 exception: tyrannosaurids, in which juveniles of some species lack denticles before acquiring
597 them in adulthood (Carr & Williamson 2004). We cannot completely rule out a single Skye
598 theropod species that underwent a tyrannosaurid-like ontogenetic change in denticle
599 development, but consider it unlikely. The Skye teeth are much older, and from theropods only
600 very distantly related to, the Late Cretaceous tyrannosaurids, which (uniquely among known
601 theropods) underwent extreme ontogenetic changes as they grew from svelte hatchlings into

602 colossal, robust, deep-skulled, incrassate-tooth-bearing, bone-crunching adults (Carr 1999;
603 Brusatte *et al*. 2010).

604 Although we cannot discount the idea that the three Skye teeth belong to the same
605 species, if this were so then this species would have displayed highly unusual ontogenetic
606 variation that is otherwise known in only one clade of highly specialized theropods living ca.
607 100 million years later (tyrannosaurids). The teeth therefore probably reflect at least two
608 species: a smaller taxon represented by NMS G.2018.17.2 and one or more larger taxa
609 represented by NMS G.2018.17.1 and GLAHM 125390a.

610

611 **Discussion**

612

613 The new teeth described here help to clarify the diversity of theropod dinosaurs on the Isle of
614 Skye. Although these specimens are extremely limited and difficult to assign to theropod
615 groups, at a minimum they support the presence of two different types of theropods inhabiting
616 the deltaic and lagoonal environments of Middle Jurassic Skye.

617 Both new specimens, NMS G.2018.17.1 and NMS G.2018.17.2, can be assigned to
618 neotheropods, based on their size, distal curvature, ziphodont morphology, and serrated edges
619 (along with the previously described GLAHM 125390a). Classifying them into particular
620 theropod groups is more difficult. The cladistic and morphometric (DFA) analyses provide
621 conflicting results, which are perhaps not surprising given that the teeth are incompletely
622 preserved, can be assessed for only a small proportion of the measurements or characters in the
623 analyses, and cannot even be identified with confidence as mesial or lateral teeth. That being
624 so, by considering the cladistic and DFA results alongside a survey of key qualitative
625 characteristics of the teeth, we can narrow down the most likely classifications for each tooth
626 among Neotheropoda.

For NMS G.2018.17.2, we conclude that it belonged to a small-bodied individual (i.e., a small-sized species or a juvenile of a larger taxon) and was probably a member of one of a few major clades (i.e., coelophysoid, ceratosaur, piatnitzkysaurid, allosauroid, tyrannosauroid). NMS G.2018.17.1, on the other hand, belonged to a larger animal that is probably either a non-abelisauroid ceratosaur, a megalosauroid, or an allosauroid. Our reanalysis of GLAHM 125390a suggests that this specimen most likely belonged to a non-maniraptoriform theropod, possibly a megalosauroid or an allosauroid, and possibly even the same species as NMS G.2018.17.1 (and, although unlikely, the same species as NMS G.2018.17.2).

The teeth from Skye are small clues that fit into a growing understanding of dinosaur evolution during the Middle Jurassic. This was a critical time in theropod history, as the more uniform faunas of the Late Triassic and Early Jurassic gave way to new species of different sizes, morphologies, and behaviours. These included apex predator megalosauroids and allosauroids that grew to over a ton in body mass, primitive human-sized tyrannosauroids that established the lineage that would eventually produce *T. rex*, and derived maniraptorans that shrank in size, developed wings, and evolved into birds (reviews in: Brusatte 2012; Hendrickx et al. 2015c; Benson 2018). At present, it is difficult to assign the Skye teeth to any of these groups, although the teeth and footprints from Skye hint at a tantalizing diversity of theropods, ranging from small to large size, that filled various niches in the Middle Jurassic food chain, probably both on land and in the lagoons. Further discoveries of more complete skeletal remains on Skye may reveal more about the identities, behaviours, appearances, and evolutionary importance of these animals, which will have huge potential for understanding keystone events in dinosaur evolution.

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955

Figures

Fig. 1. Map of the Isle of Skye (Scotland), with a box denoting Brothers' Point (Rubha nam Brathairean), where the two theropod teeth described here (NMS G.2018.17.1 and NMS G.2018.17.2) were discovered. Close up map of Brother's Point, with major geological units indicated (B).

Fig. 2. Isolated neotheropod teeth from the Middle Jurassic of the Isle of Skye, Scotland. (A-J), Crown of NMS G.2018.17.1 from the Lealt Shale Formation in A, E lingual; B, linguodistal; F, labial; G, mesial; H, distal; I, apical; and basal views; with close up on C, the apical portion of the mesial carina in mesial view; and D, the distoapical denticles in linguodistal view. (K-R), Crown apex of NMS G.2018.17.2 from the Valtos Sandstone Formation in K, M, labial; N, lingual; O, distal; P, mesial, Q, apical; and R, basal views; with L, close up on distoapical denticles in labial view. A-D, K-L are photographs; E-J, M-R are CT scan renderings. Abbreviations: dca, distal carina; mca, mesial carina. All scale bars equal 1 cm; top scale bars for A-J (except C,D); bottom scale bar for K-R (except L).

Fig. 3. Classification of NMS G.2018.17.1, NMS G.2018.17.2 and GLAHM 125390a coded as lateral crowns and analysed separately in the cladistic analysis performed with the datamatrix of 145 dental characters using TNT 1.1 and a constrained tree (ci = 0.21; ri = 0.46). For details of the constraint, please see the main text. For silhouette acknowledgements, see Appendix 5.

Fig. 4. Results of the discriminant function analysis (DFA) performed at the group-level on our personal datasets of 550 teeth belonging to 71 taxa gathered into 20 groupings along the first

two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 14.113, which accounts for 59.27% of the total variation; Eigenvalue of Axis 2 = 4.794, which accounts for 20% of the total variation). 59.27% of the theropod specimens were correctly classified in their respective groups, with NMS G.2018.17.2 and GLAHM 125390a being classified as non-abelisauroid Ceratosauria and Troodontidae, respectively. The absence of mesial and distal denticles was considered as inapplicable in this analysis. For silhouette acknowledgements, see Appendix 5.

989 **Table**

990

Datasets	NMS G.2018.17.1		GLAHM 125390a	
	Clade level	**Taxon level**	**Clade level**	**Taxon level**
Whole dataset	Neovenatoridae	*Rugops*	Troodontidae	*Rugops*
Whole dataset (no denticles = ?)	Troodontidae	*Rugops*	Troodontidae	*Majungasaurus*
Personal dataset	Neovenatoridae	*Megaraptor*	Troodontidae	*Megaraptor*
Personal dataset (no denticles = ?)	Non-abelisauroid Ceratosauria	*Arcovenator*	Troodontidae	*Majungasaurus*
Whole dataset with large teeth	Non-abelisauroid Ceratosauria	*Torvosaurus*		
Whole dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	*Arcovenator*		
Personal dataset with large teeth	Non-abelisauroid Ceratosauria	*Torvosaurus*		
Personal dataset with large teeth (no denticles = ?)	Non-abelisauroid Ceratosauria	*Arcovenator*		
Smith and Lamanna's (2006) dataset (No ratios, with CA2, DAVG2)	Carcharodonto-sauridae	*Dilophosaurus*	Ceratosauridae	*Ceratosaurus*
Smith and Lamanna's (2006) dataset (No ratios and no CA2, DAVG2)	Ceratosauridae	*Carcharodon-tosaurus*	Carcharodonto-sauridae	*Suchomimus*
Gerke and Wings' (2016) dataset (with CHR but not CBL)	Ceratosauridae	*Carcharodon-tosaurus*	Neovenatoridae	*Neovenator*
Gerke and Wings' (2016) dataset (with CBL, no ratios)	Metriacanthos-auridae	*Carcharodon-tosaurus*	Neovenatoridae	*Neovenator*

Datasets	Reclassification Rate (RR)		Clade level	
	Clade level (%)	**Taxon level (%)**	**Axis 1 (%)**	**Axis 2 (%)**
Whole dataset	62.66	62.2	51.51	19.72
Whole dataset (no denticles = ?)	63.44	60.65	50.31	19.14
My dataset	60.91	60.91	61.03	19.59
My dataset (no denticles = ?)	59.27	61.82	58.85	20.02
Whole dataset with large teeth	60.71	58	38.38	30.53
Whole dataset with large teeth (no denticles = ?)	63.43	58.57	39.2	30.84
Personal dataset with large teeth	59.47	61.47	48.3	27.66
Personal dataset with large teeth (no denticles = ?)	62.13	61.87	56.52	24.31
Smith and Lamanna's (2006) dataset (No ratios, with CA2, DAVG2)	78.49	84.3	55.77	33.54
Smith and Lamanna's (2006) dataset (No ratios and no CA2, DAVG2)	78.2	84.88	56.29	33.99
Gerke and Wings' (2016) dataset (with CHR but not CBL)	73.73	86.57	51.46	38.12
Gerke and Wings' (2016) dataset (with CBL, no ratios)	74.33	85.97	51.26	38.01

991

992 **Table 1**. Group and taxon-level identifications of NMS G.2018.17.1 and GLAHM 125390a
993 from the various discriminant function analyses (DFAs) conducted on different datasets, with
994 reclassification rate and percentage of variance for the two principal axes for each analysis.